# AUSTRALIAN TERTIARY APATOPYGIDAE (ECHINOIDEA)

# FRANCIS C. HOLMES

15 Kenbry Road, Heathmont, Victoria 3135, Australia and Invertebrate Palaeontology, Muscum Victoria, PO Box 666E, Melbourne, Victoria 3001, Australia

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The age, stratigraphic horizon and distribution of the three known Australian apatopygids and their associated echinoid faunas are discussed. *Apatopygus vincentinus* (Tate 1891) is redescribed and restricted to the Middle-Late Eocene (Johannian-Aldingan, Bartonian-Priabonian). Two new taxa are documented: *Apatopygus mannumensis* sp. nov. from the Late Oligocene-Middle Miocene (Janjukian-early Bairnsdalian, Chattian-Serravallian) and *Porterpygus devlinensis* sp. nov. from the Early Miocene (Longfordian, Aquitanian-Burdigalian). The latter is the first fossil record of the genus.

The relationship between extant and fossil species of the family in Australia and New Zealand is reviewed, taking into account the Late Palcocene-Early Eocene occurrence of Apatopygus in the Chatham Islands, New Zealand,

Key words: Echinoidea, Apatopygidae, Tertiary, Australia, new taxa,

ALTHOUGH much has been written about the extant New Zealand type species of *Apatopygus* Hawkins 1920 (*Nucleolites recens* Milne Edwards 1836) and the extant Australian *A. occidentalis* Clark 1938, the fossil record of this genus from the Tertiary of Southern Australia has been virtually ignored.

Tate (1891) briefly described the eassiduloid *Echinobrissus vincentinus* from the Late Eocene of Aldinga, South Australia, but the species, referred to *Apatopygus* by Philip (1970), was not mentioned in the major systematic works of Hawkins (1920), Lambert & Thiéry (1924, 1925), Brighton (1929), Mortensen (1948), Kier (1962, 1966) and Baker (1983). However, reference to Tate's species, under the original binomen, appear in several 19th and 20th Century faunal lists. Clark (1946) speculated on its possible relationship to the genus *Apatopygus*, but assigned it to *Nucleolites*.

Eclinobrissus vincentinus has, in the past, included specimens from the Middle-Late Eocene and from the Late Oligocene-Middle Miocene. The first record (that can be verified by recent collecting) of the Late Oligocene-Middle Miocene form, here described as Apatopygus mannumensis sp. nov., is from Spring Creek, Torquay, Victoria (Hall & Pritchard 1896). Ludbrook (1961) first recorded its presence in the Murray River cliffs, listing 'cf. Eclinobrissus vincentinus Tate' as occurring in the upper Mannum Formation at the Mannum Pumping Station, South Australia. However, it is only in the last few years that sufficient Late Oligocene-Middle Miocene specimens have become available, following extensive

collecting in South Australia and Victoria by R. J. and F. Foster, F. C. and E. Holmes, and C. AhYee and J. Krause, to allow a detailed comparison with the Middle-Late Eocene *Apatopygus vincentinus*.

Porterpygus devlinensis sp. nov., the first fossil record of Porterpygus Baker 1983, is also based on specimens collected by R. J. and F. Foster.

### AGE, STRATIGRAPHY AND DISTRIBUTION

Middle-Late Eocene localities

Apatopygus vincentinus occurs in five Middle-Late Eocene formations in southern Australia; the Tortachilla Limestone at Maslin Bay, the lower unit of the Kingscote Limestone on Kangaroo Island and the Muloowurtie Formation on Yorke Peninsula, in the St Vincent Basin, South Australia (Fig. 1, localities 1–3); and the Wilson Bluff and Toolinna Limestones at Toolinna Cove in the Eucla Basin, Western Australia (Fig. 1, locality 4).

1. The Tortaehilla Limcstone, eonsidered the origin of Tate's syntypes from 'Aldinga', crops out in the cliffs at the southern end of Maslin Bay, north of Blanche Point, about 40 km south of Adelaide. It comprises a basal bryozoal ferruginous sand, up to 1 m thick, grading up into 1 m of richly fossiliferous limestone, which is overlain irregularly by 1 m of glauconitic fossiliferous limestone (Lindsay & Alley 1995). The formation contains a rich echinoid fauna (Appendix 1) dominated by eassiduloids.

- 2. The lowest unit of the Kingscote Limestone exposed in coastal cliffs at Kingscote, Kangaroo Island, is a course grained, yellow-buff bioclastic limestone which correlates in part with the Tortachilla Limestone (Lindsay & Alley 1995). Generally this unit, particularly at the southwestern end of the cliffs towards Brownlow Beach, contains a similar echinoid fauna to that of the Tortachilla Limestone, although there are often minor diagnostic and size differences between mainland and island specimens of the same species.
- 3. The Muloowurtie Formation, which also correlates in part with the Tortachilla Limestone (Lindsay & Alley 1995), crops out in the vicinity of Harts Mine and Muloowurtie Point, on the east coast of Yorke Peninsula, south of Ardrossan. Consisting primarily of yellow calcarcous clays and varieolored sands it disconformably overlies the Lower Cambrian Kulpara Limestone (Stuart 1970).
- 4. Philip (1970) identified *Apatopygus vincentinus* at Toolinna Cove, approximately 380 km southeast of Eucla. The specimens occur 9–25 m above sea level in the white chalky bryozoal calcarenite of the upper part of the Wilson Bluff Limestone and

in the overlying coarse grained bryozoal calcarenite of the Toolinna Limestone.

Age determination. The Tortachilla Limestone, the most time restricted of the five formations, has in the past been considered early Late Eocene (Aldingan, Priabonian, planktonic foraminiferal zone P15). However, McGowran et al. (1997) placed the Tortachilla Limestone entirely within the late Middle Eocene (Johannian–Aldingan?, Bartonian, upper P14 and lower P15 foraminiferal zones). As parts of the lower unit of the Kingscote Limestone, the lower beds of the Maloowurtic Formation, and the upper Wilson Bluff Limestone (transitional to Toolinna Limestone) correlate in part with the Tortachilla Limestone, these sections may also be of late Middle Eocene age.

At Maslin Bay, an irregular unconformable contact exists between the Tortachilla Limestone and the overlying Blanche Point Formation (Cooper 1979), the lower member of which, the early Late Eocene Tuketja Mcmber, is considered to lie in upper zone P15 (Langford et al. 1995; McGowran et al. 1997) or lower P16 (Lindsay & Alley 1995).

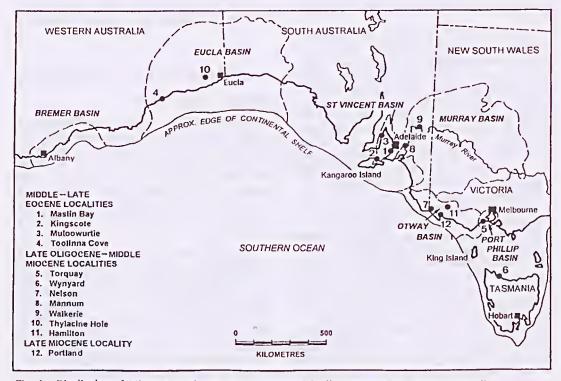


Fig. 1. Distribution of Middle-Late Eocene to Late Miocene fossil apatopygids in southern Australia.

Like the Tortachilla Limestone this member, although a ealeareous mudstone, is also glaueonitic and possibly the source of some echinoid specimens, including A. vincentinus, that have in the past been referred to the Tortachilla Limestone. Unfortunately as the exact stratigraphic horizon from which specimens have been collected is often unknown, the earliest and latest occurrence of A. vincentinus in the Middle-Late Eocene of southern Australia is still a matter of conjecture.

Although the Nanarup Limestone Member of the Werillup Formation, exposed in a small quarry at Nanarup, near Albany, Western Australia (Bremer Basin), contains an echinoid fauna similar to that of the Tortachilla Limestone, *A. vincentinus* has not yet been found (K. J. MeNamara, pers. comm.).

# Late Oligocene-Middle Miocene localities

Of Late Oligoeene-Middle Miocene localities from which *Apatopygus* is recorded (Fig. 1, locs 5-11), only the Mannum Formation in the Murray Basin (Fig. 1, loc. 8), has yielded a significant number of specimens. The Jan Juc and Puebla Formations in the Port Philip Basin (Fig. 1, loc. 5), the Freestone Cove Sandstone on the margin of the Bass Basin (Fig. 1, loc. 6), the Gambier and Port Campbell Limestones in the Otway Basin (Fig. 1, locs 7 and 11), and the Abrakurrie Limestone of the Eucla Basin (Fig. 1, loc. 10), have so far yielded only rare specimens of the genus.

- 5. About 25 km southwest of Torquay, the oldest specimens of Apatopygus mannunensis so far recorded, have been found associated with numerous specimens of Cassidulus? florescens Gregory 1892 in yellowish sandy bryozoal ealearenite of the Late Oligocene-earliest Miocene? (Janjukian) Point Addis Limestone Member of the Jan Juk Formation, which erops out in coastal eliffs at Split Point, Aircys Inlet. Near the mouth of Spring Creek, Torquay, the Early Miocene Zeally Limestone Member of the Puebla Formation (Longfordian-?Batesfordian) is exposed in low eliffs at the back of the surf beach, about 200-300 m southwest of Point Danger, where Actapericulum with A. mannumensis occurs bicarinatum Holmes 1995 in a narrow band about 1 m above beach level.
- 6. Near Wynyard, on the north coast of Tasmania, a single poorly preserved specimen almost certainly attributable to *Apatopygus* has been found in the Early Miocene Freestone Cove Sandstone (Janjukian), the lower of the two calcareous marine formations of the Table Cape Group exposed at Fossil Bluff (Quilty 1972). The Freestone Cove

Sandstone and overlying Fossil Bluff Sandstone contain a unique, although sparse, echinoid fauna which includes *Echinolampas tatei* Lambert 1898; *Monostychia etheridgei* (Johnston 1877), and *Schizaster lualli* MeNamara & Philip 1980.

- 7. In southwestern Victoria, a small quarry in the Gambier Limestone, about 1.6 km north of Nelson, has yielded small poorly preserved echinoids that fit the general diagnosis of *Apatopygus*. These specimens are associated with the neolampadoids *Actapericulum bicarinatum* and *Notolampas flosculus* Philip 1963, and, based on the age of the Gambier Limestone outcrops in the vicinity, are Early Miocene (Longfordian-?Batesfordian) in age (Abele, pers. comm., in Kenley 1971). A single partial specimen, also probably *Apatopygus*, has been found in a quarry of similar age approximately 5 km northeast of Mount Gambier.
- 8. Specimens of Apatopygus mannumensis sp. nov. from the Mannum area, two-thirds of which were eollected within 6 km of the town, are from the bioelastie ealeareous sandstone and sandy limestone of the Early Miocene (Longfordian) upper Mannum Formation, exposed in road euttings and eliffs along the Murray River between Wongulla and Mannum. In spite of an extremely rich echinoid fauna (Appendix 2), the only other eassiduloids recorded in the formation are Cassidulus? florescens (a single specimen), three species of Echinolampas, and Studeria elegans (Laube 1869), although both the neolampadoids Actapericulum bicarinatum and Notolampas flosculus are also present. Brown & Stephenson (1991), interpreted the Mannum Formation, Morgan Limestone and Pata Limestone as one lithological unit, the Mannum Limestone; the lower part encompassing the lower and upper Mannum Formation of Ludbrook (1961). This interpretation of the Mannum Limestone which includes the two marked biostratigraphie zones generally referred to as the Mannum Formation and Morgan Limestone (Appendix 2) was adopted by Rogers et al. (1995). However, Lukasik & James (1998) have now divided the Mannum Limcstone, Murray Group of Ludbrook (1961) and Brown & Stephenson (1991), into six formations, retaining the original Mannum Formation as a separate lithological unit.
- 9. On the north side of the Murray River to the east of Waikerie, about 115 km northeast of Mannum, Apatopygus nuantumensis sp. nov. and Porterpygus devlinensis sp. nov. occur in the upper Mannum Formation. Associated with large Monostyclia sp., Pericosmus compressus (Dunean

1877) and Studeria elegans, as well as Lovenia forbesii (Tenison Woods 1862), Ortholophus woodsi (Laube 1869) and several brissid species, they occur in a strongly eroded soft limestone band about 4.5 m above the level of the river flats (R. J. Foster, pers. comm.).

10. Philip (1970) recorded A. vincentinus in the Late Eocene of the Eucla Basin and also noted its presence in the Early Miocene Abrakurrie Limestone at Thylacine Hole, just over 100 km east of Eucla. As the latter locality contains a Janjukian–Longfordian fauna, it is more than likely that the specimen listed by Philip is in fact A. mannumensis, although it has not been examined.

11. Richly fossilifcrous brown and grey to dark grey silty marls of the Middle Miocene (Baleombian-Bairnsdalian) Muddy Creek Marl Member, a marginal member of the Port Campbell Limestone (Abele et al. 1988), crop out along the banks of Muddy Creek east of Hamilton, Victoria. These beds, although renowned for their rich molluscan fauna, also contain a diverse, but poorly recorded, echinoid fauna including *Apatopygus*. A single encrusted specimen has also been found in the underlying yellow brown to reddish brown limestone of the early Middle Miocene (Batesfordian) Bochara Limestone Member.

Age determination. Apatopygus mannumensis is recorded from the Late Oligocene-earliest Miocene (Janjukian, Chattian-Aquitanian, planktonic foraminiferal zones P22?-N4) to at least the Middle Miocene (late Balcombian-early Bairnsdalian, Serravallian, zones N10-N12). Inconsistences remain in recent publications concerning the stratigraphic range and correlation of Oligocene-Miocene formations with southeastern Australian regional stages and with international planktonic foraminiferal zones, particularly in the Australian Janjukian and Longfordian stages. However, McGowran et al. (1997) and Li et al. (1999) have gone some way towards rectifying these problems.

#### Late Miocene locality

12. A single 10.1 mm long specimen of *Apatopygus* found recently in the whitish chalky Late Miocenc (Mitchellian, Tortonian) Port Campbell Limestone, in coastal cliffs northeast of Nun's Beach, Portland (Fig. 1, loc. 12), is the youngest known Australian Tertiary representative of the genus. This section of the Port Campbell Limestone corresponds to the upper part of the

planktonic foraminiferal zone N16 and the basal part of zone N17 (Singleton et al. 1976).

#### MATERIALS AND METHODS

Material on which this study is based in housed in Museum Victoria (specimen numbers prefixed NMV P) and the South Australian Museum (prefix SAM P). Some secondary material examined for statistical analysis and evidence of distribution is currently held in the private collections of F. C. and E. Holmes, C. AhYee and J. Krause, and A. Anderson. Measurements were made with a dial calliper to an accuracy of 0.1 mm. Parameters are expressed as a percentage of test length (%TL) followed by the mean, the standard deviation (SD) and the number of specimens measured (N).

# SYSTEMATIC PALAEONTOLOGY

Order CASSIDULOIDA Claus, 1880 Family APATOPYGIDAE Kier, 1962

Emended diagnosis. Test small to medium, longer than wide; apical system tetrabasal or monobasal, petals weakly or moderately developed, ambulacral plates beyond petals single pored, periproct supramarginal in groove; bourrelets incipient to slightly developed, phyllodes single pored with up to three rows of pores in each half ambulacrum, no buccal pores; demiplates (pyrinid plates) may be present in ambulacra beyond petals; no naked granular zone in interambulacrum 5. Triphyllous pedicellariae with a medium internal keel and dentate margin.

Genera and range. Apatopygus Hawkins, Late Palcocene to Recent; Porterpygus Baker, Early Miocene to Recent.

Remarks. While Australian fossil apatopygids generally fit Baker's (1983: 164) emended familial diagnosis, a further revision is necessary as Apatopygus mannumensis sp. nov. and the extant A. occidentalis Clark 1938 have relatively small tests, and A. vincentinus (Tate 1891) and the extant A. recens (Milne Edwards 1836) have the beginning of a third series of phyllode pores in one or both halves of the paired ambulacra. In addition, demiplates are variably present in fossil specimens and often restricted to the adoral surface. Lack of a naked granular zone adorally on the midline of interambulacrum 5 is considered to be a familial, rather than a generie trait.

# Genus Apatopygus Hawkins, 1920

Type species. Nucleolites recens Milne Edwards, 1836 (extant) from New Zealand; original designation.

Emended diagnosis. Test small to medium, ovoid to subcircular at ambitus, low to moderately inflated; apical system tetrabasal or monobasal with four gonopores; petals narrow, open, usually conjugate; pyrinid plating in adoral and sometimes adapical ambulacra beyond petals: periproct supramarginal in groove extending to postcrior margin; peristome shallow to deep, bourrelets incipient to weakly developed, phyllodes single pored, not widened, with two or possibly three series of pores in each half ambulacrum.

Remarks. This diagnosis accommodates the two fossil species, A. vincentinus and A. mannumensis, which are considerably more variable than the extant species on which previous diagnoses have been based.

# Apatopygus vincentinus (Tate, 1891)

Figs 2A-J, 3A, D, F, 6H, 7A, D

Echinobrissus vincentinus Tate 1891: 280.—Gregory 1892: 435.

Cassidulus vincentinus (Tate).—Chapman 1915: 45. Nucleolites vincentinus (Tate).—Clark 1946: 354 (part.). Apatopygus vincentinus (Tate).—Philip in Lowry 1970: 183, (?non 186), pl. 5.—Holmes 1991: 19, figs 2D, 5A-B.

non Apatopygus vincentinus (Tate).—Sadler, Pledge & Morris 1983: 11.

Lectotype. SAM T266H from 'Aldinga', South Australia, the best preserved of Tate's eleven syntypes, is here chosen as lectotype.

Paralectotypes. SAM T266A-G and 1 from the type locality and SAM T266J and K from uncertain localities. SAM T266K is not conspecific with the rest of Tate's specimens but is a specimen of A. mannumensis.

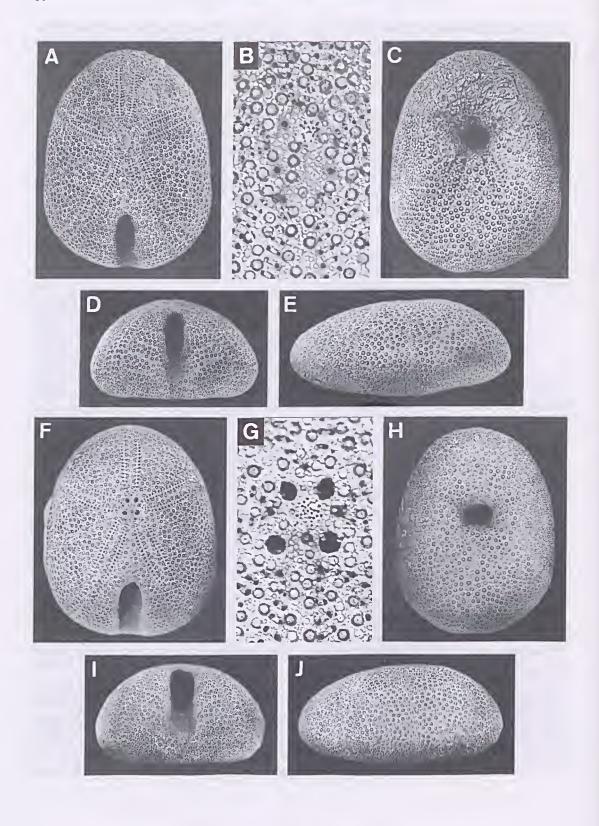
Other material. NMV P20220, 53186, 53189, 53190, 79371–79374, 82021, 82022 from 'Aldinga'; NMV P147943–147947 from 'Aldinga Bay'; NMV P133075, 148350–148362 from Maslin Bay; SAM P3328A–E from 'Aldinga Bay'; SAM P21955A–C, 22649A–C, 31804A and B, 35353A–E, 35355A and B from Maslin Bay; SAM P35354A and B purportedly from the River Murray eliffs but considered to be from Maslin Bay. Although a large number of specimens are registered as being from 'Aldinga' or 'Aldinga Bay', all specimens, including types (unless otherwise noted), are considered to be from the late Middle to early Late Eocene (Johannian–Aldingan, Bartonian–Priabonian) Tortaehilla Limestone, north of Blanche Point, Maslin Bay. Tate's specimens SAM T266J and K were not used in statistical analysis.

The following separately analysed specimens from the lower unit of the late Middle to early Late Eoeene (Johannian-Aldingan, Bartonian-Priabonian) Kingscote Limestone, Kingscote, Kangaroo Island, were used for comparative purposes: NMV P29501, 133074, 148363–148384; and SAM P35356A and B.

Diagnosis. Small to medium sized, low to moderately inflated, ovate with transversely concave adoral surface. Apical system and peristome anterior and equidistant from anterior ambitus. Petals moderately developed, paired petals extending about halfway to margin, unpaired petal three-fifths to two-thirds. Primary tubercles closely spaced adapically. Peristome deeply sunken, transversely elliptical to subpentagonal, marginally wider than long. Periproct elliptical, steeply angled and partly overhung by test at anterior end of long, deep, anal groove.

Description. Test 12.6–28.9 mm long (mean = 19.3 mm, SD = 3.6, N = 48), ovoid at the ambitus but with sides only narrowing slightly for about half the distance between the widest point and the anterior margin and with the posterior margin flattened or indented medially. Maximum width 69-84% TL (mean = 78.0%, SD = 3.0, N = 40) between 53-67% TL from the anterior ambitus (mean = 60.8%, SD = 2.9, N = 33), posterior to the apex and anterior to the anal groove. Aboral surface low to moderately inflated, transversely convex, gently curving upwards from evenly rounded anterior and lateral margins to a maximum height of 35-49% TL (mean = 41.8%, SD = 3.6, N = 33) between 50-62% TL from anterior ambitus (mean = 56.7%, SD = 3.1, N = 21). Between apex and posterior margin the aboral surface is more steeply curved, a few specimens tending to be obliquely truncated in the vicinity of the anal groove. Adoral surface slightly concave transversely between the anterior and posterior margins, mildly depressed around the well of the peristome, the degree of concavity depending on the extent of swelling of interambulacra 1 and 4 below the ambitus. Primary tubercles small, sunken, crenulate, perforate, closely spaced adaptically and around margins with progressively wider spacing adorally towards peristome, particularly in interambulacrum 5.

Apical system, tetrabasal?, with four gonopores, centre situated 36-42% TL from anterior ambitus (mean = 37.6%, SD = 1.4, N = 29). Gonopores small; hydropores, situated proximal to gonopore 2, variable in number, maximum of 32 recorded in two specimens, 19.6 and 23.2 mm long. Ocular pores 1 and V furthest from centre of apical system.



Petals moderately developed, flush, fairly narrow, straight, open distally; posterior pair longest; anterior pair shortest. Posterior paired petals extending 44-57% of the radius (mean = 51.5%), measured from centre of apical system along perradial suture to the ambitus; anterior paired petals 45-61% of radius (mean = 53.2%); anterior unpaired petal 57-70% of radius (mean = 62.6%). Anterior paired petals diverge 130-148° (mean = 139°); posterior paired petals 300–316° (mean = 309°). Inner pore of pore pair round, outer pore round to marginally oval, pore pair spacing about 4 per millimetre, interporiferous zone 1.5-2.0 times width of pore pair. Maximum number of pore pairs 24 in ambulaera I and V, 19 in II, III and IV (specimen 22.1 mm long).

Phyllodes not expanded, only weakly developed; pores in shallow pits form biserial rows in each half ambulacrum in II, III and IV, tending to triserial in I and V; first pore in the inner series situated just inside the well above the peristome (Fig. 3A). A small number of closely spaced non-perforate pits also occur between the inner series of pores close to the peristome. Adoral plate structure of ambulacra visible on one or two speeimens, with demiplates only evident on one of these (Fig. 3D). Ineipient bourrelets present.

Peristome anterior, transversely elliptical to subpentagonal, with posterior edge slightly flattened, length 7-12% TL (mean = 8.1%, SD = 1.0, N = 23), width 9-13% TL (mean = 10.8%, SD = 0.9, N = 22), at base of moderately to deeply sunken well with granulated sides, 37-42% TL to centre from anterior ambitus (mean = 39.4%, SD = 1.1, N = 33).

Periproct 6–10% TL wide (mean = 8.2), longitudinally elliptical and angled at more than 45° to the horizontal at the anterior end of a deep anal groove, length 3.0–4.5 times width, extending to the posterior margin. Forward edge of periproct opening is below and anterior to the vertically visible end of the anal groove which is situated 61–75% TL from anterior ambitus (mean = 69.5%, SD = 3.6, N = 36). Base of the anal groove may rise above posterior edge of periproct opening before curving down to posterior margin.

Remarks. Statistical analysis is based solely on measurement of specimens from the type locality

at Maslin Bay. Speeimens from Kingscote, Kangaroo Island, fall within the limits of the species but generally have a wider and higher test (Fig. 5B), less concave adoral surface, and marginally shorter anal groove with steeper angled periproct (Fig. 5D).

Apatopygus vincentinus is distinguishable from the extant type species A. recens by its more restricted size range, narrower test, more anterior apical system with fewer hydropores, and much narrower peristome. It also differs from the extant A. occidentalis by having shorter petals in ambulaera I and V, more widely spaced primary tubercles, a transversely elongated peristome, and a steeper angled periproet. A. vincentinus has greater anal groove length/width ratio, and far greater distance between the posterior margin and the posterior edge of the periproet than either extant species. It is also highly probably that the two species have different apieal plate structures; A. occidentalis being described by Baker (1983) monobasal, while an adult specimen of A. vincentinus from the Kingscote Limestone (Fig. 3F) and one from the Tortachilla Limestone elearly show a tetrabasal system.

The difference between A. vincentinus and A. occidentalis are based purely on a comparison with Baker's (1983) description, measurement and illustration of the latter.

In South Australia, Apatopygus vincentinus usually occurs with two other Late Eocene cassiduloids, Australanthus longianus (Gregory 1890) and Eurhodia australiae (Duncan 1877), that share many similar eassiduloid features. However, the latter forms are easily distinguished from Apatopygus vincentinus by their more posterior periproct, well developed phyllodes and bourrelets, and wide naked or pitted zone adorally on the midline of interambulacrum 5. A comparison with A. mannumensis sp. nov. is given below.

# Apatopygus mannumensis sp. nov.

Figs 3B, E, 4A-E, 7B, E

Nucleolites vincentinus (Tate).—Clark 1946: 354 (part.). Apatopygus vincentinus (Tate).—Sadlers, Pledge & Morris 1983: 11.

Fig. 2. Apatopygus vincentinus Tate. A, C-E, adapical, adoral, posterior and lateral views (x3.3), and B, detail of apical system (x13) of lectotype SAM T266H, from the Middle-Late Eocene Tortachilla Limestone, Aldinga Bay (?Maslin Bay); F, I, J, adapical, posterior and lateral views (x3), and G, detail of apical system (x13) of NMV P148364, and H, detail of apical system of NMV P148370 from the Middle-Late Eocene Kingscote Limestone, Kingscote, Kangaroo Island.

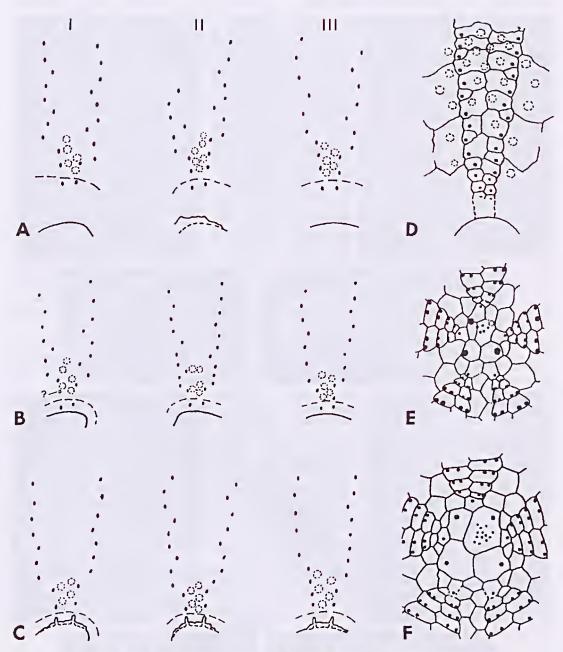


Fig. 3. A-C, phyllode pore arrangement in ambulacra I, II and III (×I2); D, demiplate (pyranid) plate structure in adoral ambulacrum III (×8); and E and F, apical plate structure (×16). A, D, F, Apatopygus vincentinus (Tate); A, NMV P148362 and D, SAM T266D from the Middle-Late Eocene Tortachilla Limestone, Maslin Bay, and F, NMV P148377 from the Middle-Late Eocene Kingscote Limestone, Kangaroo Island. B, E, A. mannumensis sp. nov.; B, NMV P148496 and E, NMV P148391, from the Early Miocene Mannum Formation, near Mannum. C, Porterpygus devlinensis sp. nov.; NMV P148399, from the Early Miocene Mannum Formation, near Waikerie. In A-C, edge of recess above peristomal opening is indicated by long broken line and non-perforate pits by broken circles.

Etymology. From Mannum, a Murray River town near which the majority of specimens were collected,

Holotype. NMV P148496 from the Early Miocene (Longfordian, Aquitanian?-Burdigalian) Mannum Formation, Cowirra Swamp Road, near Mannum; collected by J. Krause and C. AhYec, April 1996.

Paratypes. NMV P148385 and 148386 from Coolcha Landing, Younghusband; NMV P148387 from Caurnamont; NMV P148388 from Walker Flat; NMV P148389 and 148390 from Underwood Hill Road, Mannum; NMV P148391–148395 from side of road 3.4 km NE of Mannum. All from the Early Miocene Mannum Formation, South Australia.

Other material. Thirteen other specimens (currently held in private collections) from the Early Miocene Mannum Formation near Mannum.

The following separately analysed specimens were used for comparative purposes: NMV P148404 and 148405 from the Late Oligocene Jan Juc Formation, Point Addis Limestone Member, Aireys Inlet; NMV P148406–148408 from the Early Miocene Puebla Formation, Zeally Limestone Member, Point Danger, Torquay; NMV P148409–148411 from the Early Miocene Gambier Limestone, Nelson; and SAM P27908 from an unknown locality and horizon, Murray River cliffs.

Diagnosis. Small, moderately inflated, ovate, with transversely concave adoral surface. Apical system

and peristome anterior, the latter further from the anterior ambitus. Petals poorly developed, paired petals extend less than halfway to margin, unpaired petal just over halfway. Primary tubercles moderately spaced adapically. Peristome in shallow depression, transversely elliptical, wider than long. Periproet longitudinally elliptical, moderately angled at anterior end of long, shallow, anal groove.

Description. Test 9.1–14.5 mm long (mean = 11.3 mm, SD = 1.4, N = 23), elliptical to ovoid at the ambitus with posterior generally rounded and only rarely indented medially. Maximum width 74-82% TL (mean = 77.9%, SD = 1.9, N = 21) at 51-65% TL from the anterior ambitus (mean = 59.0%, SD = 3.5, N = 19), about halfway between the apex and the anterior end of the anal groove. Aboral surface mildly inflated, transversely covex, gently eurving upwards from evenly rounded anterior and lateral margins but flattening out in vicinity of apex. Maximum height 37-48% TL (mean = 43.2%, SD = 2.8, N = 21) at 48-56% TL from anterior ambitus (mean = 53.6%, SD = 1.7, N = 16). Aboral surface evenly curved between apex and posterior margin. Adoral surface mildly eoneave transversely between anterior and posterior margins, slightly depressed around the peristome.

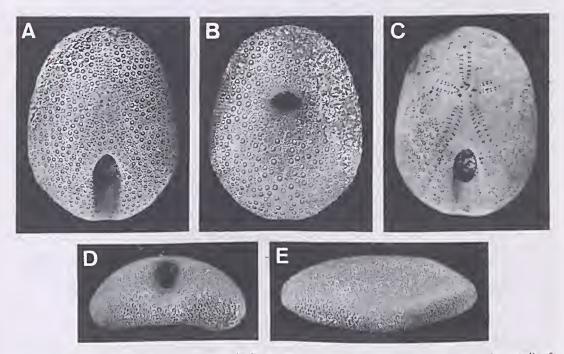


Fig. 4. Apatopygus mannumensis sp. nov. A, B, D, E, adapical, adoral, posterior and lateral views (x4) of holotype NMV P148496, and C, adapical view (x5.5) of paratype NMV P148393 from the Early Mioeene Mannum Formation, near Mannum.

Primary tubercles moderately small, sunken, crenulate, perforate, fairly widely and evenly spaced over the whole test, marginally further apart adorally.

Apical system, anterior, centre situated 33–38% TL from anterior ambitus (mean = 35.3%, SD = 1.2, N = 15). A tetrabasal (ethmophract) apical system plate arrangement, visible on only one 13.1 mm long specimen (Fig. 3E), with 4 medium sized gonopores and large pierced ocular plates, posterior pair, I and V, in contact with each other. Specimens show 5–12 hydropores proximal to gonopore 2.

Petals flush, narrow, short, straight, open distally; posterior pair longest; anterior pair shortest. Posterior paired petals 41–53% of radius (mean = 45.6%), measured from centre of apical system along the perradial suture to the ambitus; anterior paired petals 38–54% of radius (mean = 46.3%); anterior unpaired petal 47–65% of radius (mean = 55.3%). Anterior paired petals diverge 138–153° (mean = 145°); posterior paired petals 306–312° (mean = 309°). Pores round; pore pair spacing about 4 per millimetre, interporiferous zone 1.5–2.0 times width of pore pair. Maximum number of pore pairs 17 in ambulacra 1 and V, 12 in II and IV, and 13 in III (specimen 13.1 mm long).

Phyllodes not expanded, barely developed; pores in shallow pits form biserial rows in each half ambulacrum with the first pore of the inner series just inside the slight depression around the peristome (Fig. 3B). A small number of closely spaced non-perforate pits occur between the inner series of pores close to the peristome. Adoral plate structure of the ambulacra is unknown. Bourrelets incipient.

Peristome anterior, transversely elliptical, sometimes with lateral edges pointed and posterior edge slightly flattened, length 7–11% TL (mean = 9.0%, SD = 1.0, N = 15), width 11–16% TL (mean = 13.0%, SD = 1.3, N = 17), situated in shallow depression 38–42% TL to centre from anterior ambitus (mean = 39.4%, SD = 1.1, N = 198).

Periproct longitudinally elliptical, with anterior edge sometimes pointed, horizontally 12-19% TL long (mean = 16.5%), 8-13% TL wide (mean = 10.8%); opening angled  $30-40^\circ$  to the horizontal at the anterior end of a long shallow anal groove with length 2.8-4.0 times width, extending to the posterior margin. Anterior end of anal groove 58-67% TL from anterior ambitus (mean = 63.5%, SD = 2.5, N = 21).

Remarks. Statistical analysis used in the description is based on specimens collected from the vicinity of the Murray River between Walker Flat and Mannum (Mannum Formation). Other

scparately analysed Late Oligocene and Early Miocene specimens from near Torquay (Jan Juc and Puebla Formations), and from Nelson (Gambier Limestone), are comparable with the new species, showing only very minor variations in periproct size and anal groove length.

Although previously considered a small form of A. vincentinus, A. mannumensis differs by having relatively shorter petals in ambulacra II, III and IV, and relatively longer petals in I and V; more divergent anterior paired petals; more evenly and wider spaced primary tubercles; a shallow, marginally wider and often transversely pointed peristome; and a much longer, shallower anal groove with a wider and lower angled periproct, not anteriorly overhung by the test (Fig. 7E).

Like A. vincentimus it differs from extant A. occidentalis in anal groove length and distance of periproct from the posterior margin. In addition A. mannumensis has a less posteriorly located maximum test width and, unlike A. occidentalis, does not have a semicircular peristome or very elosely spaced primary tubereles.

A. mannunensis has a strong superficial resemblance to the small neolampadid Actapericulum bicarinatum with which it is sometimes found; however, the latter species is recognisable by well developed bourrelets and a lack of petals.

#### Genus Porterpygus Baker, 1983

Type species. Porterpygus kieri Baker, 1983 (extant) from near Three Kings Islands, New Zealand; original designation.

Diagnosis. Sec Baker (1983: 164)

# Porterpygus devlinensis sp. nov.

Figs 3C, 6A-G, 7C, F

Etymology. From Devlins Pound, an early settlers' trap for mustering horses on the river flats, near where the specimens were found.

Holotype. NMV P148399 from the Early Miocene (Longfordian) Mannum Formation exposed in cliffs on the right bank of the Murray River about 16 km east of Waikerie (NMV PL3430).

Paratypes. NMV P148396-148398, 148400 and 148401 from the type locality.

Diagnosis. Small to medium, low, ovate, with transversely concave adoral surface. Apical system and peristome anterior, the former much closer

to the anterior ambitus than the latter. Petals moderately developed, eomparatively long, flush, fairly narrow; paired petals extending three-fifths distance to margin, unpaired petal just over twothirds. Primary tubereles closely and evenly spaced. Peristome in shallow depression, transversely sub-

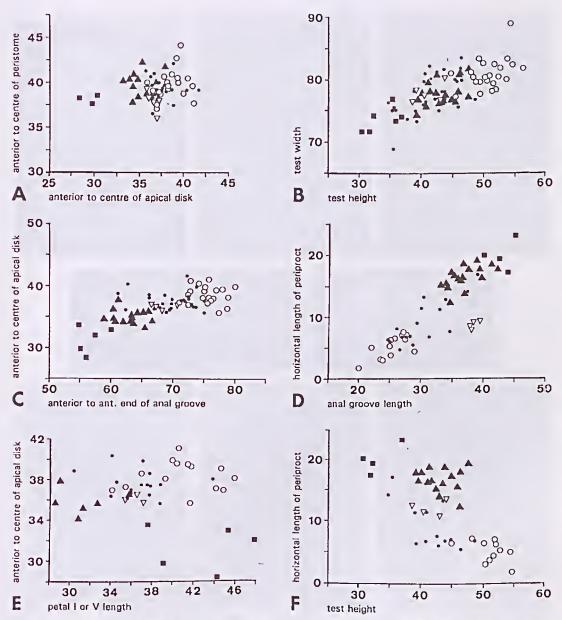


Fig. 5. Comparative biometric data on specimens of Apatopygus vincentinus (Tate) from the Middle-Late Eocene Tortachilla Limestone, Maslin Bay (•), and Kingscote Limestone, Kangaroo Island (O): A. mannumensis sp. nov. from the Early Miocene Mannum Formation, near Mannum (▲), and the Late Oligocene-earliest Miocene Jan Juc and Late Early Miocene Puebla Formations, near Torquay (∇): and Porterpygus devlinensis sp. nov. from the Early Miocene Mannum Formation, near Waikerie (■). Both vertical and horizontal scales show data as a percentage of the specimens test length.

circular to subpentagonal, slightly wider than long.

Periproct longitudinally elliptical with sharply

rounded ends, moderately angled at anterior end of a very long, wide, shallow anal groove.

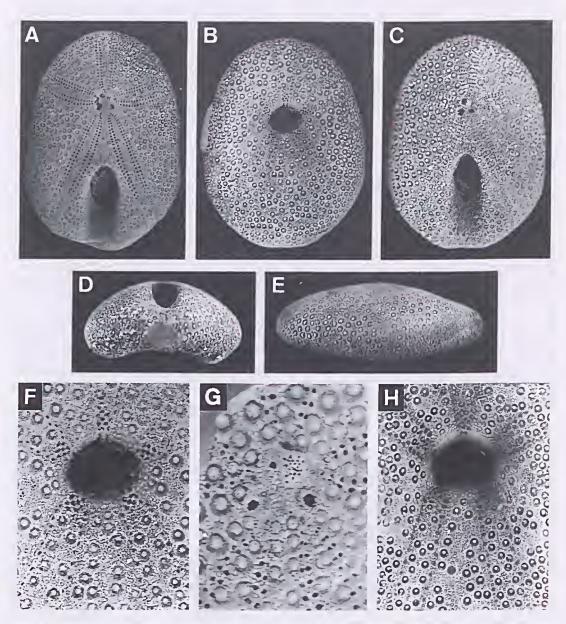


Fig. 6. Porterpygus devlinensis sp. nov. A, adapical view (×2.4) of paratype NMV P148396; B, adoral view (×3) and F, detail of peristomal area (×7) of holotype NMV P148399; C, D, adapical and posterior views (×4) of paratype NMV P148401; E, lateral view (×3.5) of paratype NMV P148400; and G, detail of apical system (×12) of paratype NMV P148398. All from the Early Miocene Mannum Formation, near Waikerie. Apatopygus vincentinus Tate. H, detail of peristomal area (×4.5) of NMV P79374 from the Middle-Late Eocene Tortaehilla Limestone, Aldinga Bay (?Maslin Bay).

Description. Test 14.6-24.3 mm long (mean = 19.3 mm, SD = 3.5, N = 6), ovoid at the ambitus but with posterior margin flattened or indented medially. Maximum width 72-77% TL (mean = 73.6%, SD = 1.6, N = 6) at 56-65% TL from anterior ambitus (mean = 59.8%, SD = 2.9, N = 6)

just posterior to the anterior end of the anal groove. Aboral surface low, transversely convex, gently curving upwards from sharply rounded anterior and lateral margins. Maximum height 32–37% TL (mean = 35.1%, SD = 1.9, N = 4) at 44–54% TL from anterior ambitus (mean = 49.2%, SD = 3.5,

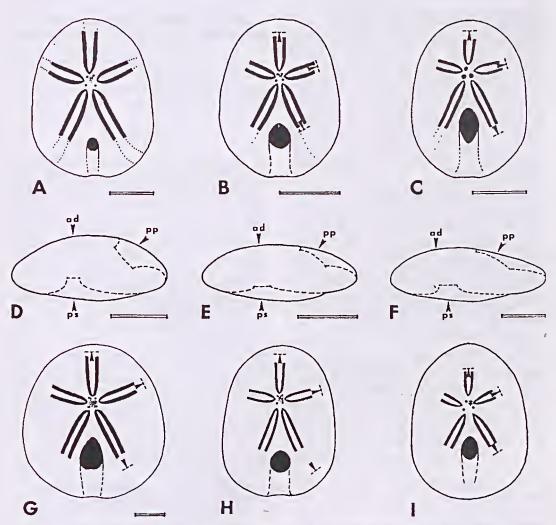


Fig. 7. Comparative drawings of fossil and recent apatopygids in adaptical (A-C, G-I) and lateral (D-F) views; scale bars 5 mm. Apatopygus vincentinus (Tate), A, SAM T266H and D, NMV P147947, from the Middle-Late Eocene Tortachilla Limestone, Maslin Bay; A. mannumensis sp. nov., B and E, NMV P148496, from the Early Miocene Mannum Formation, near Mannum; Porterpygus devlinensis sp. nov., C, NMV P148401 and F, NMV P148399, from the Early Miocene Mannum Formation, near Waikerie; Apatopygus recens (Milne Edwards), G, recent from new Zealand; A. occidentalis Clark, H, recent from Western Australia; Porterpygus kieri Baker, I, recent from New Zealand. Arrows on adaptical views show approximate maximum recorded petal lengths of species (where greater than specimen figured); broken lines and arrows on lateral views indicate centre of apical disk (ad), periproctal recess (pp) and peristomal recess (ps). Figs H and I adapted from Baker (1983).

N = 4). Between the apex and the sharply rounded posterior margin the aboral surface is mildly truncated in the vicinity of the anal groove. Adoral surface mildly concave transversely between the edges of the anterior and posterior margins and in addition slightly depressed around and posterior to peristome. Primary tubercles small, sunken, erenulate, perforate, moderately close and evenly spaced overall but with closer spacing just below the ambitus and wider spacing in depression around peristome.

Apical system with three gonopores, centre between 28–34% TL from anterior ambitus (mean = 31.2%, SD = 1.8, N = 6). Although gonopores 1, 3 and 4 are present, 4 sometimes posterior to 1, due to poor preservation the apical plate structure can only be tentatively described as tetrabasal. Hydropores variable in number, with a maximum of 23 in a specimen 20.1 mm long, situated proximal to interambulacrum 2. Large gonopores in two out of the six known specimens, suggests dimorphism.

Petals flush, fairly narrow, generally straight, mildly divergent in ambulaerum III, and open distally. Posterior paired petals much longer than others (mean = 42% TL), anterior pair (mean = 25% TL) only marginally shorter than unpaired petal (mean = 25% TL). Anterior pair of petals diverging at 146–156° (mean = 151°), posterior pair at 308–314° (mean = 310°). Pores round; pore pairs approximately 3 per mm, interporiferous zone about twice the width of the pore pair. Maximum number of pore pairs 26/27 in ambulaera 1 and V, 17/18 in ambulaera II, III and IV (specimen 24.3 mm long).

Phyllodes not expanded, barely developed, single pores tend to form uniserial rows in each half ambulaera l, III and V, but biserial rows in II and IV; first pore in each half ambulaerum just outside the slight depression around the peristome. Narrow slits, in line with the two rows of pores between the weakly developed bourrelets, occur in the edge of the test around the peristome opening (Fig. 3C). Between the rows of pores elose to the peristome are a small number of non-perforate pits. Adoral plate structure of ambulaera not known.

Peristome anterior, subcircular to subpentagonal, slightly wider than long, centre about 38% TL from anterior ambitus.

Periproet longitudinally elliptical, with anterior and posterior ends sharply rounded, about 20% TL long and 12% TL wide, angled 30–35° to the horizontal at the anterior end of a very long, wide and shallow, anal groove which just reaches the posterior margin. Anterior end of anal groove 55–60% TL from anterior ambitus (mean = 56.8%.

SD = 1.9, N = 5), posterior edge of periproet 20–26% TL (mean = 22.8%, SD = 2.4, N = 4) from posterior margin.

Remarks. Porterpygus devlinensis sp. nov. is only the second recorded species of the genus and the first from the fossil record. While superficially very similar to the extant type species P. kieri, it differs in having a far more anterior apieal system, a shallower less anterior peristome, considerably longer petals, a steeper angled periproet, and a less sharply rounded posterior margin (Fig. 7C). Its three gonopores and much longer posterior paired petals distinguish it from the Early Miocene Apatopygus mannumensis, with which it occurs in the upper Mannum Formation.

#### DISCUSSION

The tetrabasal apical system in what must be considered adult specimens of the Late Paleocene-Early Eocene Apatopygus sp. from the Chatham Islands, New Zealand (A. aff. recens of Brighton 1929; 311, fig. 2); the Middle-Late Eocene A. vincentinus, and the Late Oligocene-Middle Miocene A. mannumensis from South Australia (Fig. 3E, F); support the suggestion by Suter (1994b), in a cladistic analysis of living eassiduloids, that the ontogenetic character of the apical system in the extant A. recens (tetrabasal in immature specimens, monobasal in adults) is derived. Further, Mooi (1990: 70, fig. 1) figured an adult specimen of A. recens over 40 mm long with a tetrabasal apical system in which each of the four genital plates contain multiple hydropores. However, this latter configuration appears suspect, particularly in view of the figures published by Mortensen (1921: 187, fig. 21a, b) which infer that the ontogenetic fusing of the plates, leading towards a monobasal system, follows the development of the madreporite. Whether the development of the apical system of the small extant Australian species A. occidentalis is similar to A. recens is unknown, no immature specimens having been recorded.

This evidence, together with the occurrence of a tetrabasal apical system in the Early Miocene *Porterpygus devlinensis* and the extant *P. kieri*, refutes the statement made by Kier (1962) that eassiduloids rapidly changed from a tetrabasal to a monobasal system in the Late Cretaceous and that such a change was (in adult specimens) all inclusive.

That nucleolitids are ancestral to the apatopygids has never been seriously disputed, Kier (1962) having erected the latter family only because the apatopygids have single pores and pyrinid plating in the ambulaera beyond the petals, features, with the partial exception of *Oolopygus*, not found in nucleolitids. Mortensen (1948) even considered 'the great stress laid by Hawkins (1920) on the ambulaeral structure, particularly the so-called "Pyrinid" structure', to be greatly exaggerated; a fact supported by this study. Smith (1984: fig. A.1) showed the Nucleolitidae extending from the earliest Middle Jurassic to the present day, presumably to incorporate the Apatopygidae, a family which he does not mention or include in his classification of the Echinoidea.

Although Suter (1994a) noted that the results of eladistic analyses of cassiduloid phylogeny are ambiguous and analysis of morphological characters demonstrate extensive, but not excessive, homoplasy among cassiduloid genera, his figured consensus trees and eladograms, in particular his preferred phylogenetic hypothesis, closely link the apatopygids (based on the characteristics of the three extant species) with a small group of Cretaceous–Early Paleogene nucleolitids. From this eladistic evidence, Suter concluded that the extant apatopygids are a small remnant of the same paraphyletic stem group to more recent elades (e.g. the eassidulid, faujasiid echinolampadid and neolampadid–oligopygoid–elypeasteroid elades).

Morphological variation within fossil apatopygids is fairly pronounced between groups of specimens from different populations (Fig. 5) making any definitive link between fossil and extant species a matter for speculation. However, the

three southern Australian species of *Apatopygus* probably constitute a single lineage, although there are no distinct evolutionary trends evident, with the exception of a general decrease in size and reduction in the number of hydropores. Indeed, based on some characteristics it is possible that the extant *A. occidentalis* is more closely related to the Middle–Late Eoeene *A. vincentinus* than to the Late Oligocene–Middle Miocene *A. mannumensis*.

The relationship between Australian and New Zealand species of the genus is even more difficult to postulate, Suter (1994b) concluded that Apatopygus is probably not monophyletic. There is little evidence that the extant A. recens is a descendant of either of the two fossil species, even though the Australian Early Miocene Porterpygus devlinensis and the New Zealand extant P. kieri, each found associated with Apatopygus, seem to be very closely related.

Confirmation of Apatopygus, Giraliaster and Echinolampas in the Late Paleocene-Early Eocene strata of the Chatham Islands (Campbell et al. 1993), echinoids comparable with those found in the Middle-Late Eocene of southern Australia (Fig. 8), raises further questions as to the early diversification of Apatopygus, particularly as the Chatham Island occurrence pre-dates that in Australia by more than 12 million years. While this occurrence and that of the eidarid Eucidaris, which is also found in the Chatham Islands, represent the first record of these genera, Giraliaster first appears in the Middle Paleocene

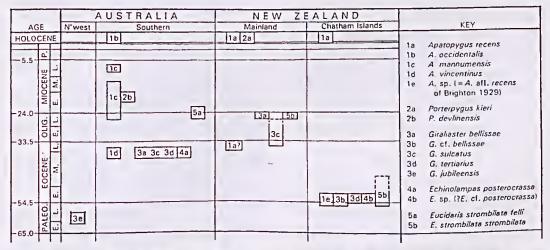


Fig. 8. Stratigraphic range of apatopygids in the Cenozoic of Australia and New Zealand compared with that of cehinoid genera known to occur in the Late Paleocene–Early Eocene strata of the Chatham Islands. Data based on Foster & Philip (1978), Baker (1983), Campbell et al. (1993) and current research (see 1ext).

Cardabia Formation of the Carnarvon Basin, Western Australia (K. J. McNamara, pers. comm.) and *Echinolampas* in the Paleocene–Early Eocene of North Africa, Pakistan and Madagascar (Roman 1965).

Except for a single schizasterid species found subsurface in the Perth Basin (McNamara 1993), there is no record of the southern Australian Paleocene-Early Eocene echinoid fauna that must have existed. Outcrops of marine sediments from this period of time are restricted to the Late Paleocene Pebble Point Formation in the Otway Basin of Victoria which, although containing a fairly rich molluscan fauna, is devoid of echinoids (T. A. Darragh, pers. comm.). Without such a record it is impossible to say whether the Chatham Islands echinoids are, at least in part, linked to any southern Australian fauna as the result of intermittent trans-Tasman migration during the Paleocene-Early Eocene; well before the accelerated opening of the oceanic gap between Australia and Antarctica and the onset of major marine transgressions over continental margins that commenced in the late Middle Eocene. The first substantiated easterly trans-Tasman migration of echinoids took place during the early-mid Tertiary; two species of Giraliaster from the Middle-Late Eoccne of southern Australia also being recorded from the latest Eocene-Oligocene of mainland New Zealand (Foster & Philip 1978).

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Appendix 1. Middle-Late Eocene echinoids recorded from the Tortachilla Limestone (St Vincent Basin), South Australia.

#### Cidaroida

Stereocidaris cudmorei Philip 1964

S. fosteri Philip 1964

S. intermis Philip 1964

S.? hispida Philip 1964

S.? intricata Philip 1964

S. sp. 'C' Philip 1964

Salenidia tertiaria (Tate 1877): Philip 1965

#### Temnopleuroida

Ortholophus bittneri Philip 1969 Tatechinus nudus Philip 1969

#### Clypeastcroida

Fibularia gregata Tate 1885

#### Cassiduloida

Apatopygus vincentinus (Tate 1891) Australanthus longianus (Gregory 1890)

Echinolampas posterocrassa Gregory 1890; McNamara & Philip 1980

Eurhodia australiae (Duncan 1877): Philip 1970

# Neolampadoida

Aphanopora? bassoris Holmes 1995: Holmes, unpub, ident.

Pisolampas concinna Philip 1963

#### Holastcroida

Giraliaster bellissae Foster & Philip 1978

G. sulcatus (Hutton 1873): Foster & Philip 1978

G. tertiarus (Gregory 1890): Foster & Philip 1978

# Spatangoida

Gillechinus cudmarei Fell 1963: McNamara, Philip & Kruse 1986

Hemiaster (Bolbaster) subidus McNamara 1987

Linthia pulchra McNamara 1985

Prenaster aldingensis Hall 1907: Philip 1970

Protenaster preaustralis McNamara 1985

Psephoaster lissos McNamara 1987

Schizaster (Paraster) tatei McNamara & Philip 1980

Appendix 2. Early-Middle Miocene echinoids recorded from the Mannum Formation and Morgan Limestone (Murray Basin), South Australia. Man. = Mannum Formation; Mor. = Morgan Limestone; \*? = occurrence of species in the formation, although noted in past literature, needs to be confirmed.

	Man.	Mor.
Cidaroida		
Delocidaris prunispinosa (Chapman & Cudmorc 1928), var. 'A' radioles of Philip 1964	*	*
Goniocidaris mnrrayensis Chapman & Cudmore 1934; Philip 1964	*?	*
Goniocidaris? pentaspinosa Chapman & Cudmore 1928, var. 'B' radioles of Philip 1964	*	*
Phyllacanthus clarki clarki (Chapman & Cudmorc 1934); Philip 1963		*
Menocidaris compta Philip 1963	*?	*
Arbacioida		
Murravechinus paucituberculatus (Gregory 1890): Philip 1965	*?	*
Temnopleuroida		
Cryptechinus lumilior (Bittner 1892): Philip 1963		*
Goniosigma murrayensis (Philip 1969)	*	*
Goniosigma princeps (Philip 1969)	*	
Ortholophus morganensis Philip 1969		*
Ortholophus pulchellus (Bittner 1892): Philip 1969		*
Ortholophus woodsi (Laube 1869): Philip 1969	*	
Parodoxechinus novus Laube 1869: Philip 1969 and Philip & Foster 1971	*	
Paradoxechinus profundus Philip & Foster 1971	*?	
Echinoida		
Heliocidaris ludbrookae Philip 1965	*	
Strongylocentrotus antiquus Philip 1965	*	
Clypeasteroida		
Clypeaster sp.: Holmes, unpub. ident.		*
Fibularia gregata Tate 1885	*	*?
Monostycliia australis Laube 1869	*	*
Monostychia sp. 'A': Sadler, pers. comm.	*	
Monostychia sp. 'B': Sadler, pcrs. comm.	*	
Monostycliia sp. 'C': Sadler, pers. comm.		*
Prowillungaster major Wang 1994	*	
Scutellinoides patella (Tate 1891): 1rwin 1995	*?	*
Sismondia? murravica Tate 1893	*?	*
Willungaster scutellaris Philip & Foster 1971: Holmes, unpub. ident.	*	
Cassiduloida		
Apatopygus mannumensis sp. nov.	*	
Cassidulus? florescens Gregory 1892: Holmes, unpub. ident.	*	
Eclinolampas gambierensis Tenison Woods 1867: McNamara & Philip 1980	*	
Echinolampas morgani Cottcau 1890; McNamara & Philip 1980	*	
Echinolampas ovulum Laube 1869: McNamara & Philip 1980	*	
Porterpygus devlinensis sp. nov.	*	
Studeria elegans (Laube 1869)	*	*?
Ncolampadoida		
Actapericulum bicarinatum Holmes 1995	*	
Notolampas flosculus Philip 1963	*	
Holasteroida		
Corystus dysasteroides (Duncan 1877): Foster & Philip 1976b	*	

	Man.	Mor
Spatangoida		
Amoraster tuberculata McNamara & Ah Yee 1989	*	
Brissopsis tatei Hall 1907: McNamara, Philip & Kruse 1986		*
Brissus fosteri McNamara, Philip & Kruse 1986	*	
Cyclaster archeri (Tenison Woods 1867): McNamara, Philip & Kruse 1989	*	*
Eupatagus cetus Kruse & Philip 1985	*	
Eupatagus collabus Kruse & Philip 1985	*	
Eupatagus ludbrookae Kruse & Philip 1985	*	*
Eupatagus murrayensis Laube 1869: Kruse & Philip 1985	*	
Eupatagus rotundas Duncan 1877: Kruse & Philip 1985	*	*
Eupatagus wrighti Laube 1869: Kruse & Philip 1985		*
Hemiaster (Bolbaster) planedeclivis Gregory 1890: McNamara 1987a		*
Hysteraster paragrapsimus McNamara & Barrie 1992		*
Lovenia forbesii (Tenison Woods 1862): Irwin & Archbold 1994	*	*?
Lovenia woodsii (Etheridge 1875): Irwin & Archbold 1994		*?
Pericosmus compressus (Duncan 1877): McNamara & Philip 1984	*	*?
Pericosmus celsus McNamara & Philip 1984	*	
Pericosmus sp. 'A' McNamara & Philip 1984	*	
Protenaster antiaustralis (Tate 1885): McNamara 1985	*	
Psephoaster klydonos McNamara 1987	*	
Schizaster (Dipneustes) fasteri McNamara & Philip 1980	*	
Schizaster (Schizaster) abductus Tate 1891: McNamara & Philip 1980		*
Victoriaster gigas (McCoy 1882): McNamara & Philip 1984		*?

Note: References to authors and supporting literature cited in the above appendices, but not listed in the main text references, can be found in Holmes (1993).